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IN MEMORIAM

Paul C. Mundinger, 1934–2011

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Paul C. Mundinger, a distinguished scientist and a friend of many of us who are interested in the study of vocal learning in birds, died in Rye, New York, on November 10, 2011. Paul was born on October 12, 1934, in Highland Park, Illinois. As a boy, Paul had a passion for the lives of animals, and while spending time outdoors he developed a quiet patience and keen sense of observation. He particularly enjoyed watching birds, and fishing—especially on Wisconsin lakes. He lived a fun and rather wild youth, especially during the summers when he lived in North Dakota with his grandparents, driving a car and working full-time at a summer resort when he was only 15. His father, a very conservative but deeply intellectual Lutheran minister, could never understand why his son came to accept evolution and ultimately devoted his life to its study. Paul received his B.S. in 1956 and M.S. in 1958, both from the University of Michigan, and his Ph.D., under Bill Dilger, from Cornell University in 1967. Dilger, an early pioneer in the evolution of behavior, is best remembered for his work on the heritability of nesting habits in lovebirds.

The development and evolution of learned behavior came of age as a scientific pursuit in the 1950s, when bird song was developed as a model system by two Europeans, Holger Poulsen in Denmark and William H. Thorpe in England. They took advantage of a new instrument, the sound spectrograph, which converted sounds into a visual display. This display allowed many frequency and timing features of sound to be analyzed in great detail. This technology prompted wonderful work that used birds to study basic issues about vocal learning, many of which were relevant not only to birds but also to humans. W. H. Thorpe used the new tool to make the first detailed description of vocal learning in a songbird, the Chaffinch. Thorpe showed that, as in humans, vocal imitation in this bird occurred particularly well in juveniles. Moreover, when sounds were played over a speaker, young Chaffinches imitated the songs of their own kind but disregarded those of other songbirds. That is, they had a bias to learn Chaffinch song. Inheritance shapes learning. Paul stepped into this rich emerging field in 1967 when he joined the laboratory of Peter Marler at The Rockefeller University in New York. Marler had trained under Thorpe in Cambridge and was a leader of the new integrative biological study of learning. At that time, Rockefeller shared with the New York Zoological Society a research facility at the Bronx Zoo. When Paul became a postdoctoral fellow in the Marler Laboratory, he used this joint facility and Marler's sound spectrograph to study how cardueline finches (small songbirds such as the American Goldfinch and Pine Siskin) used their vocal learning skills. He found that these birds, as adults, could closely imitate the calls of a new mate or the calls of other members of a winter flock, and that they also responded preferentially to playbacks of these calls. This work, published in 1970 in *Science*, was an elegant example of vocal learning plasticity that persisted into adulthood. Its function, Paul suggested, was to strengthen social bonds.

That same year, Paul joined the Biology faculty at Queens College of the City University of New York, where he conducted two main research programs over the next 40 years. Throughout his career he was extraordinarily dedicated to his questions, passionate to discover the answers, and driven to advance the ideas he developed. His first enterprise focused on cultural evolution, using the House Finch. This gregarious and loquacious bird had been introduced to New York in the early 1940s from its native California. The population spread through suburban neighborhoods on Long Island, mainland New York, and eventually the entire East Coast. As they spread, song dialects emerged, such that all male and female House Finches living in the same neighborhood sang similar songs, and different from those just a short distance away. Paul was fascinated by this opportunity to study the emergence of a cultural tradition in real time. He noticed that males and females engaging in courtship sang the same dialect song to each other; he suggested that they had learned this song as juveniles growing up in the same neighborhood. He thought this might be a case of local birds using song dialects as a criterion when shopping for mates, perhaps facilitating the process of pair formation and preserving local adaptations. Because of the limitations of the techniques then available, Paul was not able to test this theory.

Paul generalized from his work on cultural evolution, developing ideas that he would share and discuss with his colleagues, present to the behavioral-biology and bird-song communities, and also examine in his two favorite and longest-running courses, Animal Behavior and the Evolution of Culture—both also favorites among students. Out of this thought came several recurring questions, and a conviction that biologists studying cultural evolution would be able to answer them only by placing the study of culture firmly on a quantitative scientific basis. Paul was disappointed that Richard Dawkins's idea of memes (cultural elements), and the study of memetics—apparently so promising in 1976 with the publication of *The Selfish Gene* (Paul's favorite book)—never fully blossomed into a science, but instead degenerated into distracting talk of mind-viruses. Paul's hope was that this detour would be rectified and that memetics would flourish as a fully empirical, integrative, and hypothesis-driven social science. At the end of his courses he would raise the question, leaving the possibilities lingering in the imaginations of his students, as to whether an explanatory science of cultural evolution might guide us toward, in his words, "a mix of intelligently self-interested, democratic, and science-based policies. . . . Would such a science address and help solve big-issue problems facing the world?"

Despite his contribution to and lifelong interest in cultural evolution, Paul became convinced that a purely cultural-inheritance paradigm was too simple. He suspected that the interactive process that would later be called "gene–culture coevolution," or his preferred term "biocultural evolution," was really the way in which cultural change and diversification tended to happen, on the long view. Genes affect culture and culture affects genes, possibly yielding a feedback loop. Testing the components of such a hypothesis would require the study of the genetic basis for learned behavior, the interaction between nature and nurture. Thus, from about 1975, although he continued to record House Finches, he became increasingly convinced that he needed a different model system: a bird that exhibited behavioral variation not only due to learning, but also due to genetic variation, and one that would take well to laboratory rearing and breeding experiments. He found the ideal model in another songbird, the canary.

Canaries are native to the Canary Islands, off the western coast of Africa, from where they colonized Madeira and the Azores. Canaries have been bred in captivity for the past 500 years, and bird fanciers in different parts of Europe bred some of them for their plumage, and others for song—particularly their pitch, song length, and extent of frequency modulation. Thus, some canary breeds were artificially selected for their learned song in the same way that other animals were selected for other traits such as their meat, size, color, or skills at hunting or other work. By the 1970s, work from Peter Marler's laboratory had shown that young canaries normally learn their song by imitating adults within their hearing. These imitations were very accurate. Paul wondered how the different canary breeds, having diverged genetically, would differ in learning. Would males from one song strain—say, German rollers that were bred to sing low-pitched, "rolling" songs—be able to imitate the songs of another strain, such as Border canaries that were bred for their plumage and sing bubbly high-pitched songs much like wild canaries do? Questions like this, at the nexus of genes and learning, guided Paul's continuous breeding experiments at Queens College for more than three decades. Testament to the power of artificial selection, to this day no other animal species has been discovered to have such pronounced differences in inherited predispositions to learned behavior as Paul found in canaries.

The main results from Paul's canary research are striking and unambiguous. Given a choice of songs, canaries bred to sing low-pitched songs (e.g., rollers and waterslagers) will learn and produce only low-pitched songs. On the other hand, typical canaries, including Borders, prefer to learn high-pitched songs much like wild birds do (although they will learn more low-pitched songs if allowed to interact with birds singing them). Cross-fostering by an alien-strain female has no noticeable effect on the development of canaries' song-learning preferences, which therefore are not acquired at the nest. These results demonstrate genetic divergence of a learned behavior between strains of a species: evolution of bird song, the poster child of model systems for animal learning. This was the first study to show that a cultural trait transmitted by social learning is also modulated by genetic differences between individuals within a species. Moreover, unlike wild canaries or canaries bred for color, Paul found that birds bred to sing low-pitched songs will sing nearly normal tours (repeated syllables), though assembling them rather simplistically, even when reared in acoustic isolation! This suggests that even the relative contribution of genes and learning to song output can evolve, raising the possibility that a history of selection has led to genetic assimilation or reduction of plasticity in the song system.

Because hybrid canaries learn and sing a combination of the songs of both parental breeds, Paul's breeding experiments were able to elucidate further the genetic basis for strain-specific inherited learning predispositions, demonstrating, for instance, polygenic control and the presence of particular sex-linked and autosomal effects. His final experiments, in review as we write, showed distinct genetic effects on both song learning and production, some of which were remarkably specific, even influencing the preference of particular song elements over others.

Paul's work on song function and the interplay between nature and nurture during learning contributes to our understanding of how sexual selection can operate on a learned behavior. The primary functions of learned bird song in males are to ward off other males and to "charm" females, to use Darwin's term. For heritable biases favoring one song over another to emerge, selection must act on the predispositions and preferences of both sender and receiver. If the receiver—male or female—does not respond to a song, then regardless of any learned details that a male might put into it, it is a wasted effort. Paul's observations on canaries, House Finches, goldfinches, and siskins suggested, along with the work of others, that brain pathways for the production and perception of learned song are tightly intertwined and perhaps evolve in concert, a phenomenon also thought to occur in humans.

Paul used teaching as an opportunity to immerse his students in research and the consideration of unanswered questions in the field, often questions that he himself was engaged in addressing. For instance, each year he would give his Animal Behavior students his wild or captive canary recordings to reanalyze, individual by individual. He made clear that they were not going through the motions in a prefabricated lab exercise, but rather performing primary research, and that many of the results they would report in their lab manuals had not been published. In some cases, their professor himself did not even know what they would discover. Paul was zealous about teaching, taking inordinate time to make his lectures and labs engaging and influential. In 35 years of teaching, he never missed a class until weakened by his final illness.

Paul was an indefatigable collector of data, but his scientific thought was always devoted to the current question, about which he possessed and conveyed an intense and single-minded interest and excitement. The outcome of this research model of "overproduction and selective attrition" is a relatively small collection of dense and carefully considered publications, and an enormous repository of unpublished data, the analyzed portions having been so far presented only in lectures, dissertations, theses, and posters. For instance, did calls too diverge between canary strains, and might learning be involved in these sounds generally presumed to lack it? Did plumage and song coevolve during the history of selective breeding in canaries, and might the genes for both have migrated onto the same chromosomes in certain breeds during a history of coselection? Are there natural canary dialects between and within the islands to which the species is native? How did House Finch song diverge and what happened to the dialects he reported in New York, as the bird spread throughout the East Coast? How do House Finch songs vary across broad geographic stretches in their ancestral range (e.g., throughout California), and why did some of these features (e.g., dialects) subsequently change in the introduced population? The answers to all these questions lie in data that Paul and his students collected. Gradually, some (but not all) these data are being placed back in the pipeline and will likely yet see the light of day, or are being made available to the research community in other ways. Paul's entire extensive collection of wild bird-song recordings, for instance, are currently being accessioned into Cornell's Macaulay Library of Natural Sounds.

As much as Paul liked biology, he was a well-balanced individual and cultivated a diverse range of activities and interests. For instance, he became an expert in managing his retirement accounts and stocks, and returns on the accounts that he managed always beat the ones handled by the professionals. In his later years, his interests in physics, economics, and politics grew—on the very week of his death, he was reading *Freakonomics* voraciously and writing notes in the margins. At times, he kept a journal of his responses to national and international politics and events. He was unstoppable when he believed in something, and he spearheaded several causes in his town of Rye, New York, achieving tax reform and the protection of local wetlands. He was an avid boater and loved skiing and snorkeling.

He also took enormous pride in his family and found great pleasure in their company. In 1958, at age 24, he married Mary O'Neil, who would later achieve professional and public prominence as the Dean of the Columbia University School of Nursing, the Edward M. Kennedy Professor of Health Policy, and an outspoken defender of nursing and proponent of the nurse practitioner movement. Paul and Mary had four children: Paul (1959), a lawyer; Ann (1960), who graduated from Stanford and then Columbia School of Nursing; Tom (1962), a physiologist and diabetes researcher at the University of Washington; and Elizabeth (1964), also a lawyer; and seven grandchildren.

Paul used his life well. He enjoyed his science, loved his family, and believed deeply and acted fully in all that he did. He was incredibly generous and gracious, and yet able to conjure a storm when treated unethically. He was well liked, riveting at dinner parties, able to fascinate his neighbors and friends with his ideas and stories. His professional colleagues thoroughly liked him and admired his kindness, integrity, and devotion to his ideas. He left his mark in these relationships, in his research and teaching, in his family, and in other ways. Today his family's beautiful Rye property exhibits the perseverance and patience with which he did everything in life—he sculpted a perennial garden out of a brushy knoll, and extended the back lawn to a peaceful sandy beach that melds harmoniously into the natural waterside vegetation. Those of us who knew him and appreciate his work celebrate all he did, are grateful for it, and miss him.